

THE SILURIAN BRACHIOPOD
EOCOELIA HEMISPHAERICA
(J. DE C. SOWERBY) AND RELATED SPECIES

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ABSTRACT. The atrypaecean *Eocoelia* occurs widely in the Upper Llandovery and is now known from the lower Wenlock. It shows evolutionary trends in the progressive suppression of ribs and in the modification and strengthening of the articulatory mechanism. These trends are used to define four successive species, *Eocoelia hemisphaerica* (J. de C. Sowerby) of C₁-C₂ age, *E. intermedia* (Hall) of C₃-C₄ age, *E. curtisi* sp. nov. of C₅ age, and *E. sulcata* (Prouty) of C₆-Wenlock age. The taxa *Eocoelia hemisphaerica sefinensis* (Williams) and *Eocoelia quebecensis* Amos and Boucot are relegated to the synonymy of *Eocoelia hemisphaerica*. Because of the abundance of *Eocoelia* at some localities, the term *Eocoelia* Community seems appropriate; this community probably occurred in a near-shore environment. Brachiopod lineages, such as the *Eocoelia* lineage, provide a reliable basis for fine-scale correlation.

THE small costate atrypaecean *Eocoelia* is a characteristic element of Upper Llandovery and low Wenlock shelly deposits in Great Britain, eastern North America, and Siberia. It is also known from Norway and South America (Harrington 1950). Differences, considered to be evolutionary in nature, have been noticed in *Eocoelia* by Williams (1951) and Amos and Boucot (1963), and make the fossil an important one for correlation purposes. Material for the present investigation was collected from the southern part of the Welsh Borderland (Gloucestershire, Herefordshire, and Worcestershire) where *Eocoelia* occurs in profusion and can be obtained from many stratigraphic levels ranging in age from C₁ (early Upper Llandovery) to early Wenlock.

The type species of *Eocoelia*, *Atrypa hemisphaerica*, was originally described by J. de C. Sowerby in Murchison's *The Silurian System* (1839, p. 637, pl. 20, fig. 7). Unfortunately the locality of the figured specimen was not specifically stated. There is a specimen in the Geological Survey Museum labelled 'Sil Syst Pl. 20, f. 7.'; it resembles the figure only in being a block containing many specimens. However, the block may be accepted tentatively as the type specimen with the theory that the figure is an artist's interpretation of this block. The label on the block is Ankerdine Hill (an area in Worcestershire at the southern end of the Abberley Hills), one of the two localities mentioned by Sowerby for his species. Davidson (1866, pl. XIII, fig. 23) was probably wrong in stating the locality of Sowerby's specimen to be May Hill, a locality that was not mentioned in the first edition of *The Silurian System* (1839).

Davidson further confounded the issue by figuring specimens from several localities and inadvertently giving greater prominence to specimens which, on close examination, are quite distinct from the type. Thus, he showed enlargements of specimens from Penwhapple Glen, Ayrshire (1866, pl. XIII, figs. 29a, 30a), which, in contrast with the type, do not have discrete dental lamellae and which have relatively weak ribbing. It has been assumed by subsequent workers, namely Williams (1951, pp. 113-14), and Amos and Boucot (1963, pp. 445-7), that specimens like Davidson's Penwhapple Glen specimens are identical with the type; in each case these workers have erected new names

to describe species which, in reality, are identical with the type of *Eocoelia hemisphaerica*. These names, *Coelospira hemisphaerica sefinensis* Williams and *Eocoelia quebecensis* Amos and Boucot, must be relegated to the synonymy of *E. hemisphaerica*. However, the important fact is that Williams, and Amos and Boucot, showed that the form with strong ribs and dental lamellae is definitely earlier in date than the other, and Williams, working in the type area of Llandovery, established this date as C₁ of the Upper Llandovery.

A second species of *Eocoelia*, conspecific with the type of Hall's (1860, p. 147) *E. intermedia*, occurs in C₄ beds at Llandovery. Specimens of *E. intermedia* are similar to *E. hemisphaerica*, but possess relatively weaker ribs and display intermediate stages in the disappearance of the umbonal chambers of the pedicle valve, with the consequent disappearance of the dental lamellae as distinct entities.

The complete disappearance of the umbonal chambers as well as a further reduction in rib strength is seen in a third species, here named *Eocoelia curtisi*. Davidson's Penwhapple Glen specimens mentioned above are of this type, which occurs abundantly in the basal Damery beds of the Tortworth Inlier.

The highest Llandovery and lowest Wenlock beds of Tortworth, May Hill, and the Malvern Hills contain an *Eocoelia* with mere vestiges of ribs; the ribs occur only as faint traces in the early growth stages of the shell, that is, in the beak region. This form occurs in North America and has been described as *Eocoelia sulcata* (Prouty) (Prouty and Swartz 1923, p. 466).

Four species of *Eocoelia*, *E. hemisphaerica*, *E. intermedia*, *E. curtisi*, and *E. sulcata* may thus be recognized. All four occur on both sides of the Atlantic and their stratigraphic succession may be demonstrated in localities as widely separated as Maryland, Nova Scotia, and the Welsh Borderland.

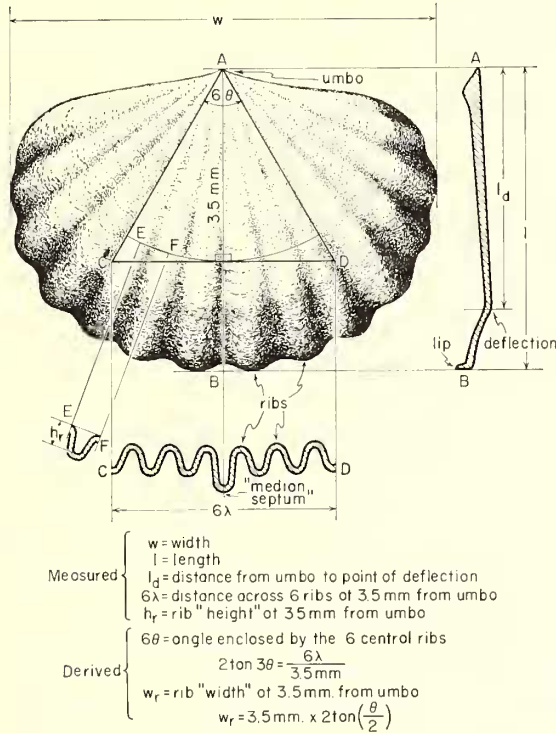
In the present investigation bulk collections were made from forty-five localities in the southern part of the Welsh Borderland and thirty-two of these contained specimens of *Eocoelia*. Numbers of *Eocoelia* range up to 272 in a collection, and the fourteen largest collections have been treated statistically (Appendix; for a description of other localities see Ziegler 1963). Collections from Llandovery and Ireland have also been examined, as well as eighty-one collections from a variety of regions in eastern North America. Such dimensions as length, width, distance between ribs at a set distance from the umbo, and height of ribs at the same distance from the umbo, were measured (text-fig. 1); also, the number of ribs was noted, as was the presence or absence of such features as the umbonal cavities and the cardinal process.

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ASSEMBLAGE ANALYSIS AND INTERPRETATION

The extent to which a fossil sample is representative of the original population is a problem which should be considered by any taxonomist who deals with closely related

species. Differences between samples cannot be used for taxonomic discrimination unless it can be shown that the samples were unaffected by current activity capable of selectively removing portions of the assemblage. Recently many techniques have been suggested for detecting preburial alteration of fossil assemblages (Fagerstrom 1964), and some of these are applicable to the *Eocoelia* assemblages preserved in the Upper Llandovery sandstones and shales of the Welsh Borderland.

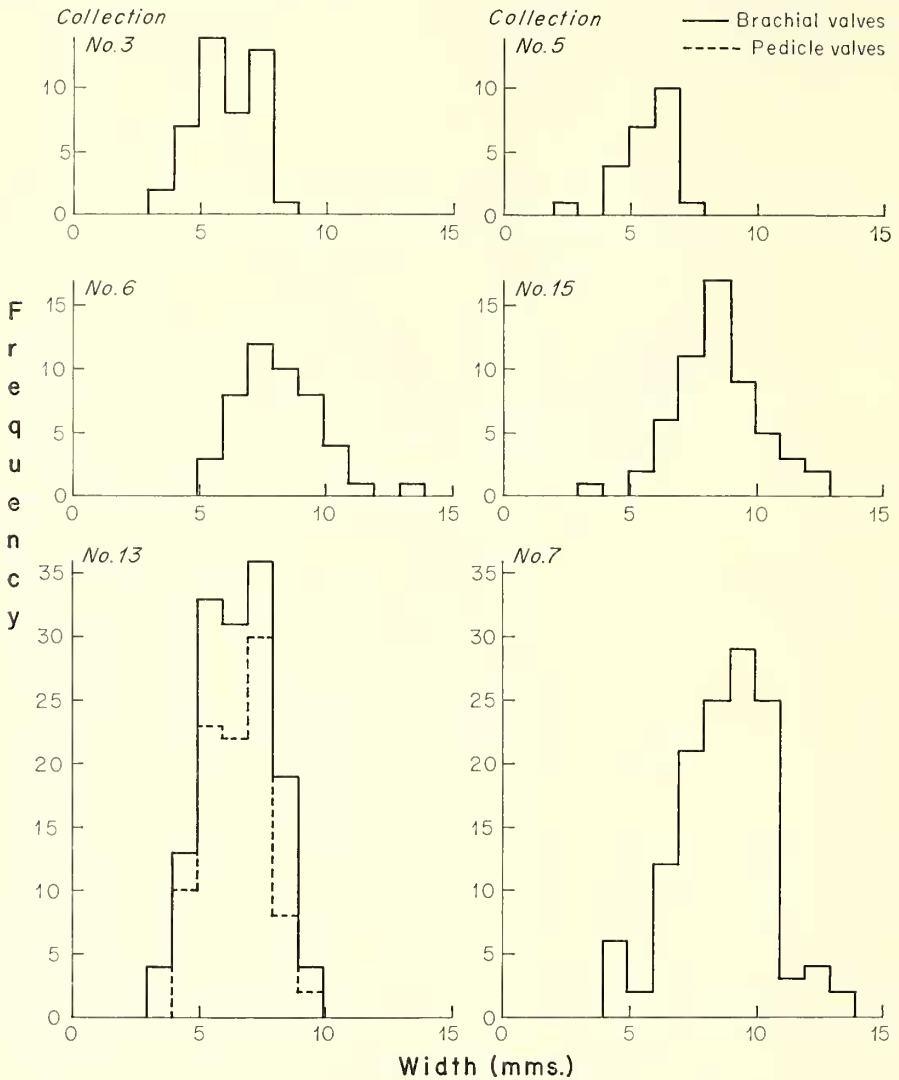


TEXT-FIG. 1. Brachial valve of *Eocoelia* showing the parameters measured.

It should be noted that the fossils of the Upper Llandovery rocks are typically confined to the bottom of some of the beds, and not evenly distributed throughout the rock either vertically through several beds or horizontally along one bed, so the activity of currents in concentrating the shells may be inferred. Furthermore, most of the valves are disarticulated; of a total of 704 brachial valves collected, only 6 remain attached to pedicle valves. This consideration is not very significant since *Eocoelia* did not possess completely locking valves, and so these would become disarticulated easily once the soft parts had disappeared. Of more concern is the fact that the ratio of opposing valves may be as high as 1:1.5. On the other hand, less than 1% of all the valves collected show signs of wear or abrasion and what little breakage exists may be largely attributed to post-burial compaction of the sediment.

The character of the size-frequency distributions has been used by some workers to distinguish sorted assemblages. Boucot (1953) theorized that undisturbed assemblages should be highly skewed to the right due to high infant mortality, while current-sorted

assemblages would have normal distributions. But Rudwick (1962) and Craig and Hallam (1963) showed that an undisturbed assemblage might very well have a modal peak in the large size range, as well as one in the very small range; this is because larvae,



TEXT-FIG. 2. Size-frequency distributions. For localities see Appendix.

once established, may have very low mortality rates until mature. The *Eocoelia* assemblages (text-fig. 2) have modal peaks in the larger size ranges; there is no peak in the small range and it must be concluded that, owing to their very small size, the victims of high infant mortality were removed or destroyed by currents.

Size-frequency distributions may be used to better advantage in another way. Since the brachial valve of *Eocoelia* is flat, or nearly flat, and the pedicle valve quite convex,

and since it is known that sphericity is an important hydrodynamic factor (Menard and Boucot 1951, p. 150), it is evident that the mean sizes of the valves would differ significantly if carried any distance by a current. The size-frequency distributions of the brachial and pedicle valves of sample 13 are compared in text-fig. 2. Although there are more brachial than pedicle valves, the shapes of the distributions correspond very closely, an indication that current sorting was at a minimum.

TABLE 1. *The relation of the Lip and Deflection to size in three collections*

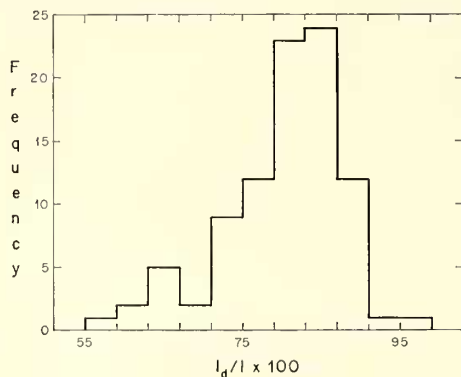
Width (mm.)	LIP					
	Collection no. 13		Collection no. 11		Collection no. 15	
	Present	Absent	Present	Absent	Present	Absent
-4.5		4		2		1
4.6-5.5	3	17	1	5		0
5.6-6.5	6	25	3	3		4
6.6-7.5	15	15	3	10		5
7.6-8.5	12	22	8	9		18
8.6-9.5	2	3	3	1		10
9.6-10.5	1				1	4
10.6-						8
DEFLECTION						
-4.5		5		2		1
4.6-5.5	17	5	2	5		0
5.6-6.5	27	7	3	4		4
6.6-7.5	23	5	10	6	1	4
7.6-8.5	31	4	9	8	7	11
8.6-9.5	5	1	4	1	8	3
9.6-10.5	1				2	5
10.6-					3	2

The examination of maturity indices may give useful information as to the relative ages represented in the samples. Two such indices, the 'lip' and 'deflection' (text-fig. 1) are present, at least in the two earlier species, *Eocoelia hemisphaerica* and *E. intermedia*. The relationship of lip and deflection to size in several samples is shown in table 1; the specimens with these structures tend to be larger, but the difference in size is by no means great and, in fact, in only the lip distribution of sample 13 is the association significant ($\chi^2 = 8.87$, $p < 0.003$). If, as seems likely, the lip is the final stage in the ontogeny of the animal, then several conclusions follow: (1) the wide size range exhibited by specimens with lips indicates that some individuals reached maturity at a considerably smaller size than others; (2) the large number of specimens with lips shows that many specimens actually lived to maturity; and (3) the fact that the specimens without lips are nearly as large as the ones with lips suggests that the former had nearly attained full maturity.

Unlike the lip, the deflection was formed some time before the animal finished growing. The distance from the umbo at which the deflection occurred (l_d) may be compared with the overall length of the valve (l) in the ratio $l_d/l \times 100$. Text-fig. 3 shows the distribution of this statistic for sample 13. The distribution has a sharp peak showing that most of the deflections occur at about 85% of the length of the valve. More important, there is no apparent correlation between l and $l_d/l \times 100$, i.e. smaller specimens have the

deflection in the same relative position as larger specimens. As with the case of the lip, this suggests that the specimens were mostly mature at the time of their death.

In conclusion, most of the fossil beds studied are thought to be the result of some event, such as a storm, which stirred up the bottom, concentrating the shells lying on the sea floor, most of which were dead and disarticulated, and burying them with a layer of sediment. There is no clear indication that current sorting seriously affected the samples, except that the victims of high infant mortality appear to be unrepresented.



TEXT-FIG. 3. Histogram showing the percentage of the length at which the deflection occurs (l = length l_d = distance from umbo to point of deflection). Measurements were made on the brachial valves of Collection 13.

SYSTEMATIC DESCRIPTIONS

Superfamily ATRYPACEA

Family LEPTOCOELIIDAE Boucot and Gill 1956

Genus EOCOELIA Nikiforova 1961

Type species. *Atrypa hemisphaerica* J. de C. Sowerby 1839, in Murchison, *The Silurian System*, p. 637, pl. 20, fig. 7.

Diagnosis. The valves of *Eocoelia* are plano-convex and effectively corrugated by prominent radial ribs. The plane of bilateral symmetry is emphasized by a strong median rib in the pedicle valve and a corresponding trough in the brachial valve; internally, this trough is a positive feature and supports a low, rounded median ridge. The articulation mechanism is developed so that, in addition to the normal tooth-socket relationship, the crural plates fit into well-defined grooves, or fossettes, on the internal surfaces of the teeth (text-fig. 4).

Comparison. *Leptocoelia* and *Australocoelia*, the two other genera of the Leptocoeliidae, always possess well-developed cardinal processes, whereas this structure, if developed at all in *Eocoelia*, is usually no more than a low inconspicuous ridge. Also, *Leptocoelia* and *Australocoelia* possess a sharply defined fold and sulcus involving two ribs of the brachial valve and one of the pedicle valve; the valves of *Eocoelia* are usually gently

warped into a fold and sulcus, but this structure is not distinct enough to be defined in terms of number of ribs involved.

Discussion. Shape. The brachial valve is usually flat, but may be gently concave or gently convex. The pedicle valve is always convex and in some cases approaches a hemispherical shape. The width is slightly greater than the length. The beak of the pedicle valve is small and overhangs the brachial valve by approximately 0.2 mm. or 0.3 mm. in specimens about 1 cm. long. Young shells tend to be equidimensional but become slightly wider with respect to their length in their older growth stages.

TABLE 2. *Statistics of the allometry curves for the variates length (l) and width (w)*

For a discussion of the parameters a , σ_a , b , and r see Kermack and Haldane 1950, p. 40, or Imbrie 1956, p. 228

Species of <i>Eocoelia</i>	Collection		a	σ_a	b	r	$l/w_{w=7} \times 100$
	no.	N					
<i>E. sulcata</i>	5	10	0.961	0.060	0.978	0.964	90.57
<i>E. curtisi</i>	9	8	1.113	0.053	0.719	0.977	89.71
	3	17	0.924	0.094	0.965	0.850	83.29
<i>E. intermedia</i>	15	16	0.817	0.042	1.218	0.972	85.29
	6	21	0.927	0.053	0.916	0.941	79.57
<i>E. hemisphaerica</i>	7	55	0.936	0.038	0.948	0.922	83.71
	11	27	1.060	0.050	0.740	0.931	83.14
	13	45	0.917	0.041	0.991	0.926	84.29
	14	11	0.851	0.100	1.159	0.890	86.71

The posterior margins form an obtuse angle at the umbo which varies from 165° to 145° as measured on the brachial valve. The delthyrium is small (from 0.2 to 0.4 mm. wide in adult specimens) and is uncomplicated by deltidial plates. The cardinal extremities are rounded. Interareas are not developed in *Eocoelia*.

Eocoelia possesses structures caused by a change in the direction of growth of the anterior margin of the shell. In one case, anterior growth ceased completely and the valves grew directly toward one another to form a 'lip' around the margin of each valve. This structure varies in height up to 0.32 mm., values of 0.1 mm. and 0.2 mm. being common (text-fig. 1). In another case, an inward 'deflection' occurs in the direction of growth of each valve (text-fig. 1). Abundant examples of the lip and deflection are to be found in the early populations of *Eocoelia*, that is, those that are grouped with *E. hemisphaerica* and *E. intermedia*, but the structures are rarely developed in the later populations, that is, *E. curtisi* and *E. sulcata*. The disappearance of these structures was gradual and is thought to represent an evolutionary trend.

There is usually a weak sulcus in the brachial valve of *Eocoelia* and a corresponding fold in the pedicle valve.

Ribs. *Eocoelia* possesses unbranching ribs which should be considered both from the standpoint of strength and number. The early species, *E. hemisphaerica*, has strong, rather angular ribs whereas the last species, *E. sulcata*, has ribs which are present only as vestiges and can be seen just in the area around the umbo, that is, in the young growth stages. The species which are intermediate stratigraphically have ribs of intermediate strength (Pl. 83).

The modal rib number varies considerably in *Eocoelia*; however, this feature does not appear to behave consistently with time (Tables 3, 4). The early species, *E. hemisphaerica*, has a moderate number of ribs with populations showing modes of 14 and 16 ribs. *E. intermedia* tends to have more ribs, the modes being 16 and 18. *E. curtisi* and *E. sulcata* have about 12 and 10 respectively, though the decrease in these cases is due as much to the progressive fading of ribs in the postero-lateral regions of the shell as to an increase in rib spacing.

TABLE 3. *Rib Number*

<i>Species of Eocoelia</i>	<i>Collection no.</i>	<i>N</i>	<i>Rib Number</i>						
			7-8	9-10	11-12	13-14	15-16	17-18	19-20
<i>E. sulcata</i>	8	5	2	2	1				
	2	3	1	1		1			
	4	5		2	1	1	1		
	5	21	3	7	9	2			
	9	7		2	4		1		
<i>E. curtisi</i>	10	8		3	2	2	1		
	3	25		1	17	6	1		
	15	18			1	12	4	1	
<i>E. intermedia</i>	6	15				1	8	5	1
	7	81			2	37	36	6	
<i>E. hemisphaerica</i>	11	8			2	5	1		
	13	79			9	52	16	2	
	14	31			9	19	3		
	12	11			2	7	2		
	*	8				7	1		

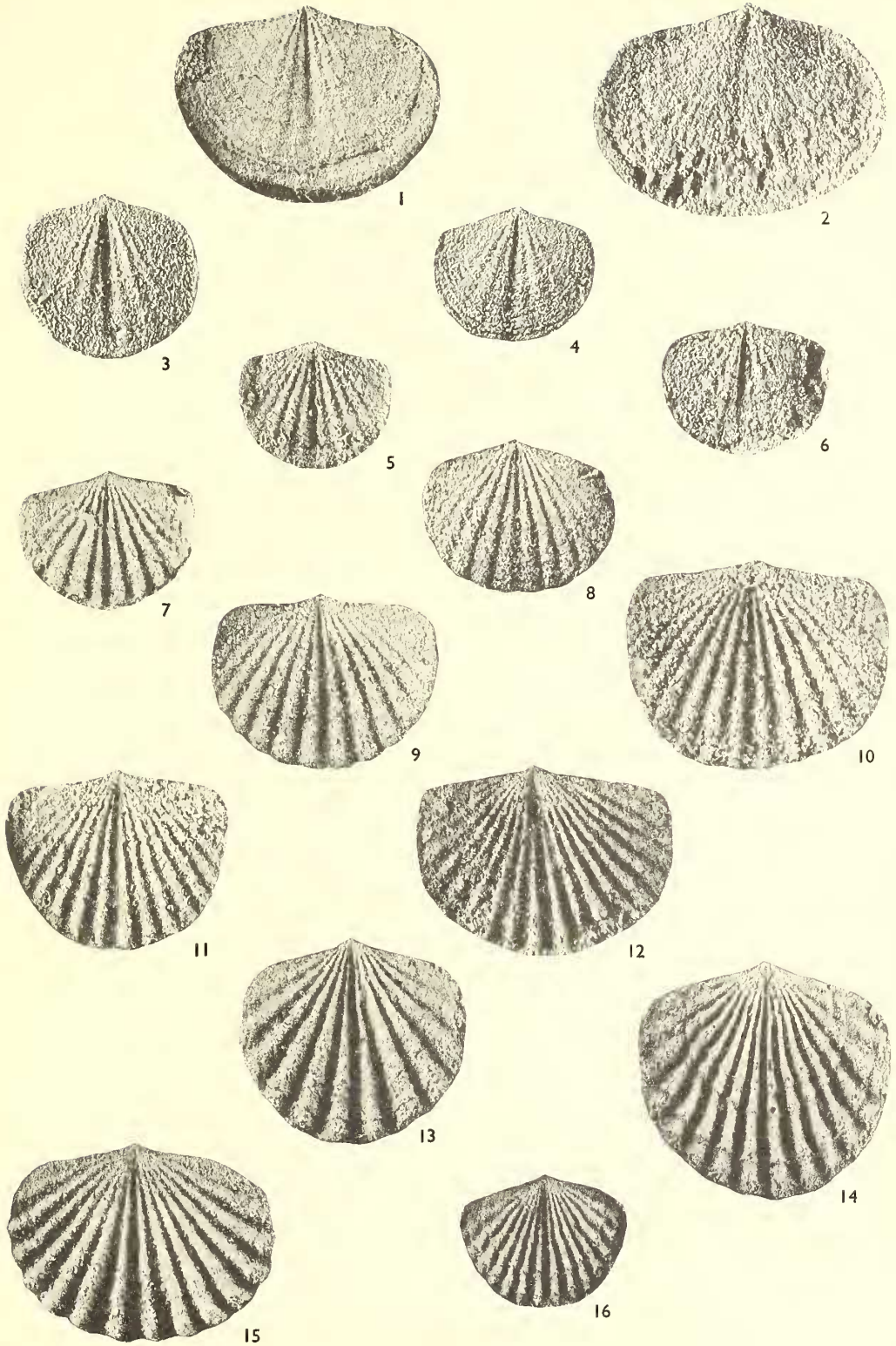
* Material from Williams's C₁ locality in the Llandovery District (1951, p. 114).

Articulation. Like most atrypids, the early species *E. hemisphaerica* possesses, in the brachial valve, a pair of blade-like hinge plates medianly bounding the sockets, and, in the pedicle valve, a pair of dental lamellae supporting teeth which are connected to the posterior margin of the shell by planareas. Lateral to the dental lamellae are umbonal chambers. However, in the later populations, these are not present and the teeth and dental lamellae are fused into one large tooth-like mass. The intermediate stage of the disappearance of these chambers is the characteristic feature of *E. intermedia* and they are never present in later populations, that is, *E. curtisi* and *E. sulcata* (Pl. 84).

The inner surfaces of the teeth of *Eocoelia* each have a groove, or fossette, into which fit the laterally directed crural plates of the brachial valve. Thus *Eocoelia* has an interlocking articulation mechanism which consists of the normal tooth-socket relationship

EXPLANATION OF PLATE 83

All specimens are rubber casts of external moulds of brachial valves, $\times 4$. For localities see Appendix. Figs. 1-6. *Eocoelia sulcata*. 1, 2, Collection 1, USNM 140431, 140432; 3, 4, Collection 8, OUM C6457a, C6454a; 5, 6, Collection 2, USNM 140433, 140434. Figs. 7-8. *E. curtisi*. Collection 3, OUM C3198b, C3225a. Figs. 9-12. *E. intermedia*. 9, 10, Collection 15, OUM C8050b, C8066b; Collection 6, OUM C1644a, C1669a. Figs 13-16. *E. hemisphaerica*. 13, 14, Collection 7, OUM C1095b, C1012a; Collection 13, OUM C6857b, C6810b.



ZIEGLER, Silurian atrypcean brachiopod *Eocoelia*

as well as the crural plate-fossette relationship. The fossettes, which are present in all species of *Eocoelia*, are more deeply impressed in the later species.

Lophophore support. Presumably the lophophore was attached to the anterior portions

TABLE 4. *Statistics of 6θ , where 6θ = angle enclosed by six ribs*

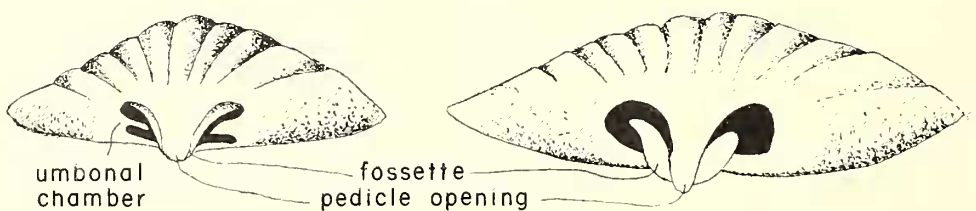
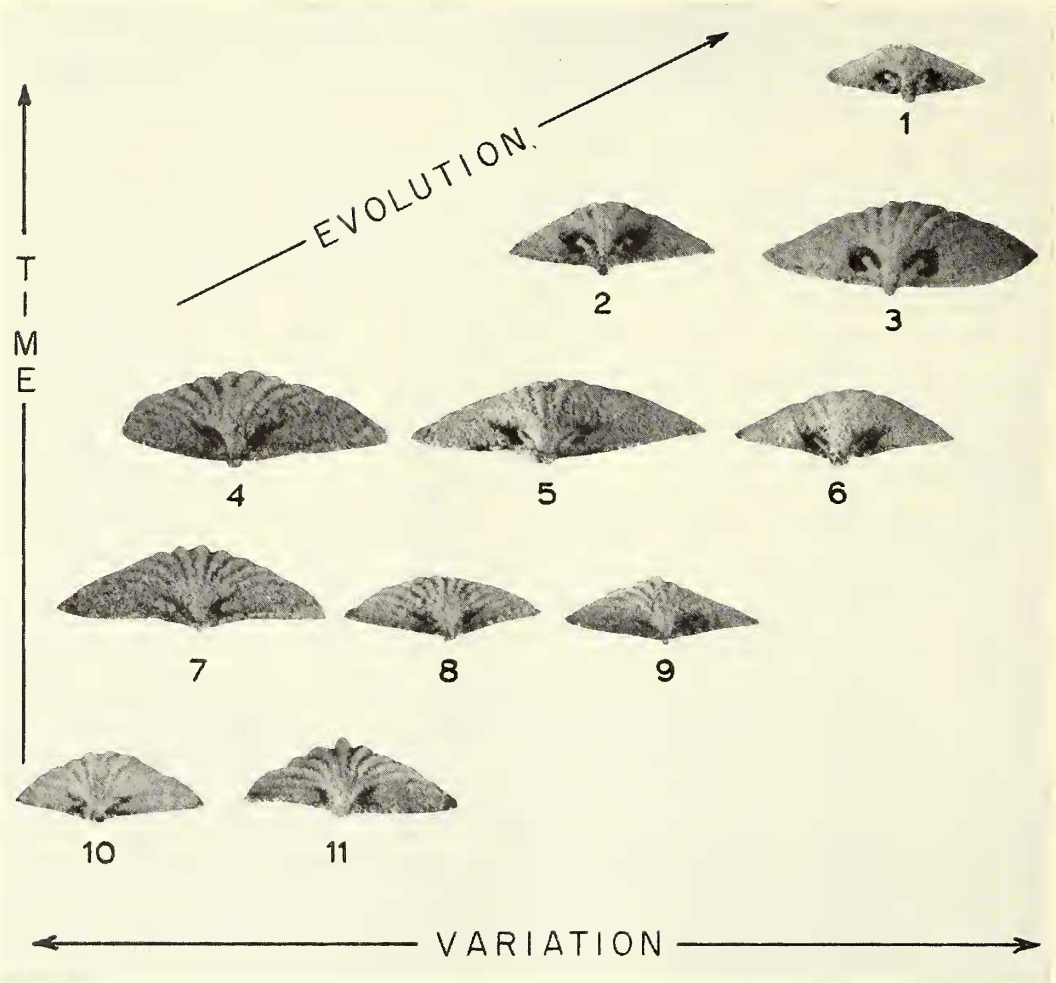
Species of <i>Eocoelia</i>	Collection		Lower confidence		Upper confidence		Standard deviation	Observed range
	no.	N	limit	Mean	limit			
<i>E. sulcata</i>	8	3	44.67	60.67	70.67	6.44	56-68	
	2	4	54.44	61.50	68.56	4.44	58-68	
	4	3	40.12	60.00	79.88	8.00	52-68	
	5	12	58.16	61.33	64.50	4.50	50-66	
<i>E. curtisi</i>	9	11	56.15	58.18	60.21	3.03	52-64	
	10	12	57.68	60.50	63.32	4.44	56-70	
	3	33	57.70	59.27	60.84	4.44	50-68	
<i>E. intermedia</i>	15	47	55.55	56.72	57.89	3.94	48-66	
	6	42	51.34	52.67	54.00	4.30	46-60	
<i>E. hemisphaerica</i>	7	114	55.85	56.88	57.91	5.56	40-70	
	11	50	57.61	59.08	60.55	5.19	48-70	
	13	94	57.88	59.17	60.46	6.29	46-74	
	14	29	57.74	60.48	63.22	5.85	52-76	
	12	14	58.65	61.57	64.49	5.06	52-78	

TABLE 5. *Statistics of the size (width)-frequency distributions*

Collection no.	N	Number of fossil beds	Mean width (mm.)	Observed range (mm.)	Description of distribution
8	6	1	6.02	4.7-7.2	—
2	9	many	6.23	5.6-7.3	—
4	7	2 or 3	7.03	5.9-8.0	—
5	23	1	5.71	2.8-7.4	skew, left
9	19	1	5.98	2.8-9.0	unimodal
10	15	several	6.68	3.0-8.6	skew, left
3	45	2	6.16	3.4-8.8	bimodal
15	56	1	8.63	3.9-12.6	skew, right
6	47	several	8.29	5.5-13.4	skew, right
7	129	many	8.87	4.2-13.8	skew, left
11	56	1	7.06	4.2-9.0	skew, left
13	141	2	6.72	3.7-10.2	bimodal
14	38	2 or 3	7.16	3.3-10.6	irregular
12	19	1	6.74	4.5-9.4	unimodal

of the hinge plates. The existence of spires has been investigated by Nikiforova (Nikiforova and Andreeva 1961, p. 253), who sectioned many specimens without finding spires, although they were present in other atrypids in the same deposit. As has been mentioned, the crural plates served in the role of articulation as well as for lophophore support. They are rather blade-like and curved laterally. The bases of the crural plates bound the notothyrial cavity and diverge anteriorly and ventrally.

Muscle attachment. In the brachial valve the adductor scars are faintly impressed immediately anterior to the crural plates and on either side of a low, rounded median



TEXT-FIG. 4. Changes in the posterior end of the pedicle valve. All specimens are internal moulds and all are $\times 4$, with the exception of the line drawings, which are $\times 8$. All the specimens are in the Oxford University Museum collections. For localities see Appendix. Top row, Collection 2, *Eoocelia sulcata*; 1, C3734a. Second row, Collection 3, *E. curtisi*; 2, C3240b; 3, C3241a (a diagram of the latter is shown in the bottom right of the figure). Third row, Collection 15, *E. intermedia*; 4, C8169a; 5, C8167a; 6, C8168a. Fourth row, Collection 6, *E. intermedia*; 7, C1719a; 8, C1702b; 9, C1699b. Bottom row, Collection 13, *E. hemisphaerica*; 10, C6937b; and 11, C7004a (a diagram of the former is shown in the bottom left of the figure).

ridge. The cardinal process (Pl. 84, fig. 5) is rarely distinct and not developed in all specimens; it is usually not more than a low ridge running along the notothyrial cavity.

In the pedicle valve, the paired diductor scars are oval with their long axes parallel to that of the valve and are sometimes impressed to such a depth that a distinct and very narrow ridge, or myophragm, is left between them (Pl. 84, fig. 4). Small elongate adductor muscle scars are often seen postero-medially to the diductor scars.

Size. *Eocoelia* is typically small, shell widths usually being under 10 mm.; the largest recorded width is 13.4 mm. The size varies considerably from collection to collection (Table 5).

Species

Atrypa hemisphaerica J. de C. Sowerby, 1839, in Murchison, *The Silurian System*, p. 637, pl. 20, fig. 7.

Leptocoelia intermedia Hall, 1860, p. 147, fig. 5.

Eocoelia curtisi sp. nov.

Coelospira sulcata Prouty 1923, p. 466, pl. 27, figs. 6–8.

Species questionably assigned

Atrypina(?) *paraguayensis* Harrington 1950, p. 62, pl. 1, figs. 9, 10, 13–16.

Eocoelia hemisphaerica (J. de C. Sowerby)

Plate 83, figs. 13–16; Plate 84, figs. 5–11

Atrypa hemisphaerica J. de C. Sowerby, in Murchison 1839, p. 637, pl. 20, fig. 7.

Atrypa? *hemisphaerica* J. de C. Sowerby; Davidson 1866, p. 136, pl. 13, fig. 23.

Coelospira hemisphaerica sefinensis Williams 1951, p. 113, pl. 5, figs. 19, 20.

Eocoelia quebecensis Amos and Boucot 1963, p. 447, pl. 62, figs. 1–10.

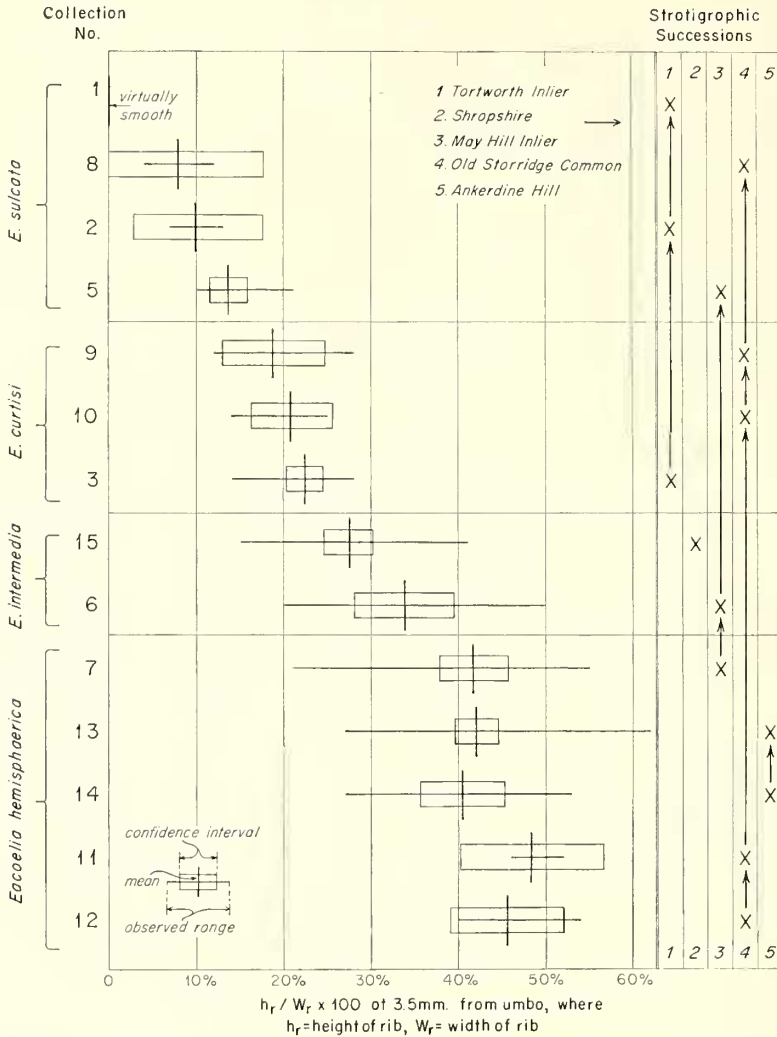
Definition. Included in this species are all populations of *Eocoelia* which consist entirely of individuals possessing umbonal cavities lateral to the dental lamellae in the pedicle valve.

Discussion. The species is strongly ribbed; the index of rib strength, mean $h_r/w_r \times 100$ (where h_r = height of rib and w_r = width of rib), for the populations identified with this species is about 40% (text-fig. 5, table 6). The individuals commonly have from 13 to 16 ribs, but may have as few as 11 or as many as 18 ribs. It should be mentioned that *E. hemisphaerica sefinensis* Williams, here synonymized with *E. hemisphaerica*, was originally said to have 12 ribs but larger collections now available clearly demonstrate a modal rib number of 14, the same as *E. hemisphaerica*; in the present work, rib counts were made only on external moulds of complete brachial valves, and failure by Williams to adhere to these standards would account for his low values.

A particularly distinctive feature of populations of *E. hemisphaerica* is the presence in many individuals of the 'lip' and 'deflection'. The lip usually occurs in about 30% of the specimens; the occurrence of the deflection is more variable and may be observed in as many as 87.5% of the individuals or as few as 15%, depending on the population (Table 7). A lip and a deflection may occur on the same specimen and occasionally two deflections are present on a single specimen. Both the lip and deflection are probably indications of maturity in *Eocoelia*; the lip would have been the final portion of the shell to grow, and the deflection usually occurs at a late growth stage of the animal, at about 85% of the shell length as measured from the umbo (text-fig. 2).

Holotype. The specimen preserved in the Geological Survey Museum (Geol. Soc. Coll. GSd 4829) is thought to be the holotype, although the artist's drawing in *The Silurian System* (pl. 20, fig. 7)

by no means confirms this. The type locality of the specimen is Ankerdine Hill, seven miles west of Worcester. The species is very abundant in this small inlier of Upper Llandoverly rocks, but *E. curtisi* also occurs on the west side of the hill between the Knightwick Sanatorium and the River Teme.



TEXT-FIG. 5. The range of variation in rib strength. The collections have been arranged in chronological order by palaeontological and stratigraphical evidence. The latter is summarized at the right of the figure. For localities see Appendix.

Occurrence. In the southern part of the Welsh Borderland, *E. hemisphaerica* occurs in the Cowleigh Park Beds of Ankerdine Hill and the Old Storr ridge Common area, both to the north of the Malvern Hills, and in the Huntley Hill Beds of the May Hill Inlier. In Shropshire the species occurs in the *Pentamerus* beds at Ticklerton, near Wenlock Edge, and at Hillend, near the Longmynd. There is a small inlier of Upper Llandoverly sandstone immediately south of Presteigne, Radnorshire, where the species occurs in abundance.

At Llandovery *E. hemisphaerica* occurs in the Sefin shales, where it has been identified as *E. hemisphaerica sefinensis* Williams (1951, p. 113); the species also occurs just to the south of this area in the bottom ten feet of the Upper Llandovery beds of the Sawdde River section.

TABLE 6. *Statistics of the rib proportions $h_r/w_r \times 100$, where h_r is the height of a rib at 3.5 mm. from the umbo and w_r is the width of the rib at 3.5 mm. from the umbo*

Species of Eocoelia	Collection no.	N	Lower confidence limit		Upper confidence limit		Standard deviation	Observed range
			Mean	Mean	Standard deviation	Standard deviation		
<i>E. sulcata</i>	8	3	0.00	7.77	17.55	3.94	4-12	
	2	3	2.01	9.87	17.73	3.16	7-13	
	3	10	11.53	13.71	15.89	3.05	10-21	
<i>E. curtisi</i>	9	6	12.98	18.84	24.70	5.58	12-28	
	10	6	16.23	20.85	25.47	4.40	14-25	
	3	15	20.23	22.37	24.51	3.87	14-28	
<i>E. intermedia</i>	15	20	24.59	27.35	30.11	5.90	15-41	
	6	13	28.14	33.82	39.50	9.40	20-50	
<i>E. hemisphaerica</i>	7	25	37.74	41.72	45.70	9.65	21-55	
	11	3	40.19	48.40	56.61	3.30	46-52	
	13	39	39.39	41.97	44.55	7.94	27-62	
	14	12	35.69	40.48	45.27	7.55	27-53	
	12	5	39.11	45.56	52.01	5.20	40-54	

TABLE 7. *Occurrence of the Lip and Deflection*

Species of Eocoelia	Collection no.	N	Lip present (%)		Deflection present (%)	
			N	(%)	N	(%)
<i>E. sulcata</i>	2	10	0	7	0	
	5	21	0	24	0	
<i>E. curtisi</i>	9	22	0	21	0	
	10	21	0	19	0	
	3	55	1.8	57	0	
<i>E. intermedia</i>	15	61	3.3	56	39.3	
	6	44	11.4	46	2.2	
<i>E. hemisphaerica</i>	7	42	28.8	40	87.5	
	11	60	30.0	71	52.1	
	13	139	30.9	145	77.9	
	14	38	36.8	47	14.9	
	12	11	27.3	24	16.7	

The species is known from the Pointe-aux-Trembles Formation of the Lake Temiscouata-Lake Touladi region of eastern Quebec where it has previously been identified as *E. quebecensis* Amos and Boucot (1963, p. 448). At Arisaig, Nova Scotia, *E. hemisphaerica* occurs in the lowest shell beds of the Ross Brook Formation at a point on the shore about 1000 ft. north-east of the mouth of Arisaig Brook.

The *Atrypina*(?) *paraguayensis* of Harrington (1950, p. 62) from beds of probable Lower Llandovery age (Wolfart 1961, p. 53) cannot at present be distinguished from *E. hemisphaerica*.

Stratigraphic range. At the type area of Llandovery, *E. hemisphaerica* occurs in the Sefin shales, an impersistent stratigraphic unit, which overlies beds of typical C₁ lithology and which was grouped with the C₁ beds by Williams (1951, p. 130). The Sefin shales contain graptolites of the zone of *Monograptus sedgwicki* (Jones 1949, p. 62) which are of early Upper Llandovery age.

The Paraguay specimens occur in beds which have been correlated with the Lower Llandovery on the basis of graptolite and trilobite evidence (Wolfart 1961, p. 53); they are the earliest known of the genus *Eocoelia*. No other Lower or Middle Llandovery occurrences are known.

The upper limit of *E. hemisphaerica* must be prior to the C₄ beds of Llandovery which contain *E. intermedia*.

Eocoelia intermedia (Hall)

Plate 83, figs. 9–12; Plate 84, figs. 1–2

Leptocoelia intermedia Hall 1860, p. 147, fig. 5.

Definition. This species includes all populations that contain individuals both with and without umbonal chambers lateral to the dental lamellae of the pedicle valve; the umbonal chambers when present are typically reduced in size by comparison with the earlier species, *E. hemisphaerica*.

Discussion. The species is distinctly ribbed, with the two populations measured showing values for the mean $h_r/w_r \times 100 \cong 30\%$. The values measured are significantly different from the larger populations of *E. hemisphaerica* measured, which are about 40%. The populations identified as *E. intermedia* show considerable variation in rib number; sample no. 6 has an unusually high mode of 16 ribs with some specimens showing as many as 20 ribs, while sample no. 15 has somewhat fewer. The ribs of *E. intermedia* show a slight tendency to fade out and disappear in the postero-lateral parts of the shell.

The lip and deflection are developed in only a few specimens.

Holotype. The type specimen of Hall's *Leptocoelia intermedia*, now preserved in the American Museum of Natural History, no. 1634, is similar to the Welsh Borderland collections, nos. 6 and 15, in rib strength and in the very reduced umbonal cavities (Pl. 84, figs. 1–2). Hall's specimen came from Arisaig, Nova Scotia, where *Eocoelia* occurs at many horizons in the Ross Brook Formation. All four species

EXPLANATION OF PLATE 84

For localities of Figs. 5–17 see Appendix.

Figs. 1–2. *Eocoelia intermedia* (Hall 1860, p. 144, fig. 5). Holotype, Arisaig, Nova Scotia. AMNH 16341:0, pedicle valve; 1, posterior view of internal mould; 2, internal mould.

Figs. 3–4. *E. sulcata*, Arisaig, Nova Scotia. AMNH 16341:1 pedicle valve; 3, posterior view of internal mould; 4, internal mould.

Figs. 5–11. *E. hemisphaerica*, Collection 13. 5, OUM C6849a, internal mould of brachial valve; note cardinal process. 6–8, OUM C6857a, brachial valve; 6, internal mould; 7, rubber cast of internal mould; 8, oblique view of rubber cast of internal mould. 9–11, OUM C6966a, pedicle valve; 9, internal mould; 10, rubber cast of internal mould; 11, oblique view of rubber cast of internal mould.

Figs. 12–17. *E. curtisi*, Collection 3. 12–14, OUM C3189b, brachial valve; 12, internal mould; 13, rubber cast of internal mould; 14, oblique view of rubber cast of internal mould. 15–17, Holotype, OUM C3241a, pedicle valve; 15, internal mould; 16, rubber cast of internal mould; 17, oblique view of rubber cast of internal mould.



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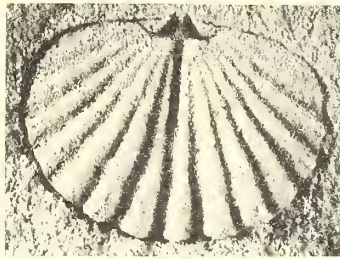
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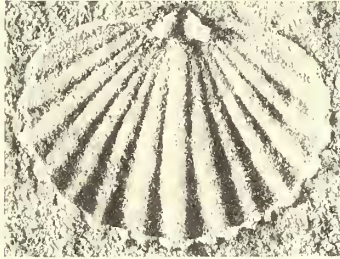
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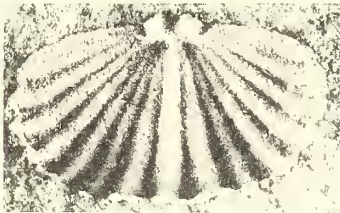
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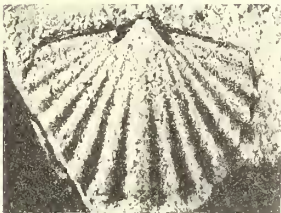
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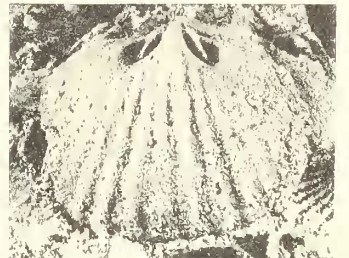
12



13



14



15



16



17

of *Eocoelia* occur in this sequence; included with Hall's type specimen in the American Museum of Natural History are some specimens with extremely weak ribs which probably came from a higher horizon than the type (Pl. 84, figs. 3-4).

Occurrence. In the Welsh Borderland *E. intermedia* occurs in the Huntley Hill Beds of May Hill, as does *E. hemisphaerica*, and in the *Peutameres* Beds of Norbury, Shropshire. At Llandovery the species occurs in beds mapped by Jones (1925) as C₄ in an old quarry just west of the road from the village of Myddfai to the farm Gorllwyn-fawr, at the point adjacent to the farm Gorllwyn-fâch.

Stratigraphic range. As stated, at Llandovery, the species occurs in beds mapped as C₄ (Jones 1925). The upper and lower ranges cannot be determined rigorously because sufficient specimens of *Eocoelia* have not yet been found in C₃ or C₅ at Llandovery. Nor can the superposition of *E. intermedia* on *E. hemisphaerica* be rigorously demonstrated; however, mapping evidence at May Hill and Llandovery suggests this relationship.

Eocoelia curtisi sp. nov.

Plate 83, figs. 7-8; Plate 84, figs. 12-17

Atrypa? hemisphaerica J. de C. Sowerby; Davidson 1866, p. 136, pl. 13, figs. 24a, b, c.

Definition. This species is defined to include populations which show no sign of umbonal chambers or dental lamellae in the pedicle valve, but which do have distinct ribs.

Discussion. The teeth of this species are broadly based on the floor of the pedicle valve instead of being supported by dental lamellae as is the case with *E. hemisphaerica* and some specimens of *E. intermedia*. Fossettes (grooves on the median sides of the teeth) are more deeply incised in *E. curtisi* than in earlier species. The fossettes are a type of socket into which fit the laterally directed hinge plates of the brachial valve.

The ribs of *E. curtisi* are weaker than in earlier species, the value of mean $h_r/w_r \times 100$ being about 20% for the populations measured. The differences with earlier populations are statistically significant in some cases. Rib number varies about a mode of 12; this decrease with respect to earlier populations is due both to a wider spacing of ribs and to the progressive disappearance of ribs in the postero-lateral regions of the shell.

The lip and deflection are virtually absent in *E. curtisi*.

Holotype. Oxford University Museum specimen no. C3241 from collection 2, Charfield Green, Tortworth Inlier (Pl. 84, figs. 15, 16, 17).

Occurrence. The species is particularly abundant in the Damery Beds of the Tortworth Inlier and may be collected at Charfield Green and Damery Quarry, localities that were frequented by the early workers. At May Hill a few specimens, probably *E. curtisi*, have been found in the Yartleton Beds. *E. curtisi* occurs in the basal Wyche Beds both at Gullet Quarry, Malvern Hills district, and at the Gunwich Mill site, Old Storridge Common. A specimen, probably of this type, has been discovered in C₅ beds at Llandovery, 500 yards north of the farm Llwyn-Meredith in a stream section. In Ireland *E. curtisi* is abundant in the lowest beds of the Annelid Grit, north-west Co. Galway.

In North America the species has been identified from Arisaig, Nova Scotia, where it occurs at the mouth of Arisaig Brook.

Stratigraphic range. *E. curtisi* probably does not range higher or lower than the C₅ beds of Llandovery. *E. intermedia* occurs in C₄ at Llandovery, and in the southern part of the Welsh Borderland *E. sulcata* occurs in the top part of the Llandovery sequences, that is, in beds that are probably equivalent to the unfossiliferous C₆ shales of the type area.

Eocoelia sulcata (Prouty 1923)

Plate 83, figs. 1–6; Plate 84, figs. 3–4

Coelospira sulcata Prouty, in Prouty and Swartz 1923, p. 466, pl. 27, figs. 6–8.

Eocoelia sulcata (Prouty), Boucot *et al.* (in press).

Definition. Populations identified with this species have vestigial ribs, that is, ribs that are present only in the young growth stages and are not apparent at the anterior commissure of the average-sized specimen.

Discussion. The index of rib strength (mean $l_r/w_r \times 100$) is very low, the values being about 10%, as compared with those of *E. curtisi*, which are about 20%.

E. sulcata is similar to *E. curtisi* as far as the structures of the beak and of the pedicle valve are concerned; that is, umbonal chambers and dental lamellae are absent.

Holotype. Prouty's specimens from the Rochester Formation and the upper part of the Rose Hill Formation of Maryland are the types of this species. It may eventually prove necessary to designate new types as Prouty's specimens cannot be located at present (G. A. Cooper, personal communication).

Occurrence. At Tortworth *E. sulcata* occurs in the Tortworth Beds, that is, the top of the Llandovery section, and in beds mapped as Wenlock (Curtis 1955, p. 4). The species occurs in the upper part of the Yartleton Beds of May Hill and in the upper part of the Wyche Beds near Old Storridge Common. In Norway, the species is abundant in Stage *Sa-b* at Gjettem Station, Baerum, Oslo-Asker District. Apart from the type localities in Maryland, the species also occurs in North America in the Long Reach Formation of New Brunswick (Boucot *et al.*, in press).

Stratigraphic Range. The superposition of beds containing *E. sulcata* on *E. curtisi* may be demonstrated at Tortworth and Old Storridge Common. Since *E. curtisi* is of C₅ age, *E. sulcata* probably originated about C₆. *Eocoelia* may have become extinct about the middle of the Wenlock as there is no record of it in the upper Wenlock or Ludlow. Amos and Boucot would derive the Devonian brachiopod *Leptocoelia* from *Eocoelia* (1963, p. 443), but the later species of *Eocoelia* show trends in the loss of ribs that make this connexion unlikely. *Leptocoelia* may have been derived from one of the early species of *Eocoelia*, which are similar in several respects, but there is no direct stratigraphic evidence for this.

PALAEOECOLOGY

Eocoelia is a widespread element in Upper Llandovery and low Wenlock faunas, but it is only really abundant at certain localities. At these localities *Eocoelia* dominates the assemblage to such an extent that the expression *Eocoelia* Community is appropriate (Ziegler 1965). The *Eocoelia* Community occurs in the Cowleigh Park Beds of Ankerdine Hill and Old Storridge Common where it is of C₁–C₂ age, in the Huntley Hill Beds of

May Hill where it is of C_1 - C_3 age, and in the Damery Beds of Tortworth where it is of C_5 age. Each of these stratigraphic units is a basal unit deposited by the transgressing Silurian sea and in each of these areas the *Eocoelia* Community is succeeded by a community dominated by *Pentameroides* sp. At Presteigne the *Eocoelia* Community is well developed in beds of C_1 - C_2 age and is succeeded by a Community dominated by *Pentamerus* sp. The *Eocoelia* Community occurs in both the Conglomerate Series of Marloes Bay, Pembrokeshire, and the Annelid Grit of Co. Galway, Ireland; in each of these places it is associated with basal beds deposited by a transgressing sea.

Owing to its association with transgressive seas, and often with relatively coarse clastic rocks, the *Eocoelia* Community is thought to represent a coastal environment. It was not the only coastal community, however, as the basal Cowleigh Park Beds of the Malvern District contain a very restricted fauna dominated by *Lingula pseudoparallela* Stubblefield, '*Camarotoechia*' *decemplicata* (J. de C. Sowerby), some bivalves and gastropods, and little else.

INTERPRETATIONS OF THE TRENDS AND VARIATIONS

The most easily understood trend in *Eocoelia* is the gradual strengthening of the articulatory mechanism. Individuals with deeper fossettes, stronger hinge plates, and larger, more broadly based teeth would have had a selective advantage, particularly in the relatively rough coastal environment inferred for this brachiopod. Trends toward increased articulation have been noticed in other brachiopods; for instance, several groups of stropheodontids independently display increases in the number of denticles along their hinge lines with time (Williams 1953b).

The reason behind the rather striking decline in rib strength is less obvious. The ribs may have originally helped in the protection of the animal by their interlocking effect. If this were so, then the development of the articulatory mechanism might well have made the ribs redundant.

Other features of *Eocoelia* disappear during the time of the development of the articulatory mechanism; both lip and deflection are unknown in the later species. The formations of these structures, seen particularly well in populations of *E. hemisphaerica*, involved changes in the direction of growth at the anterior commissure with consequent demands for rapid reorientation of the teeth in the sockets. With time, the deepening of the fossettes to produce more of an interlocking articulation may have made this reorientation difficult and eventually impossible.

There is considerable variation between collections in both the mean size and relative numbers of *Eocoelia*. Moreover, the two factors seem to be related in a positive way, that is, when *Eocoelia* occurs in large numbers, as in the *Eocoelia* Community, the individuals tend to be large; but when it occurs sporadically the individuals are always small. The fact that size and numbers are related suggests that they were originally controlled by the general favourability of the environment for *Eocoelia*.

Finally, the reasons behind the variation in the spacing of the ribs are not at present understood. It cannot yet be established whether or not variation exists between populations at one horizon. At best, it can be said that the rib spacing appears to vary in a random way in a given stratigraphic section.